ART 15. AN ANALYSIS OF COLOR AND PATTERN IN BUTTERFLIES OF THE ASIATIC GENUS *KARANASA*

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(A posthumous paper. Dr. Avinoff died July 16, 1949.)

Foreword

The major avocation of the late Dr. Andrey Avinoff, Director of the Carnegie Museum from 1926 to 1945, was the collection of butterflies and the study of their colors and patterns. To him the ultimate in rarity and interest was the group of little brown and orange Satyrids of the genus *Karanasa* from the high mountains of Turkestan, Afghanistan, and Kashmir. Over a period of forty years he studied all of the known specimens and gathered together everything that had been written concerning them. He accumulated two imposing collections, the first of which was nationalized by the Soviets and the second given to the Carnegie Museum. I worked with him in the study of these butterflies for eight years and the task of publishing the final report has been placed in my hands. Dr. Avinoff was constantly devising and revising schemes for recording and analyzing the color patterns of *Karanasa*. This one, evolved in 1945, is more or less of a digression from the main line of study of the genus. I present it separately with a minimum of editing.

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A standardization of properties in coloration and pattern of *Karanasa* lends itself to a graphic survey. A chart based on the characteristics of the front wings has been prepared (plate 1) in order to assist in analyzing the mutual relationship of coloration and pattern of the upperside. It occurs to me that the most convenient way of visualizing these characteristics, as exemplified by all possible variations in *Karanasa*, is to be obtained by a table with vertical and horizontal rows: the vertical columns stand for pattern, the horizontal for pigmentation, thus establishing a system of co-ordinates. By reducing the variety of patterns to as few types as possible it was found that the most practical subdivisions would represent the gradual intensification of the dark parts of the basal portion of the front wings. Thus, the sequence runs through the following gradations: (1) a completely light base, (2) a light base bounded by a dark band through the mesial part of the wing from the middle of the costa to the inner edge, corresponding in part to the branded portion on the wings of the males in some species, (3) a more or less uniform dark suffusion of the base, mixed with the ground color, and without a too contrasting transverse mesial

Issued October 31, 1950.

band, or (4) a completely dark base approximating in intensity the fuscous marginal area with usually a still darker outline of the discal, light, transverse band. These four divisions would practically suffice if there would not be occasionally some forms displaying a general darkening not only of the basal part but also the outer portion of the wing; the light band in such instances is much darkened, especially exteriorly. Examples of this are few but they have to be accounted for in a diagrammatic scheme and it is questionable whether such a phenomenon should be classified under the terms of pattern or coloration. Since this is an extension and spread of the dark area, it was found more advisable to consider it as a matter of pattern—in the sense of distribution of the light and dark areas on the surface of the wings—and treated accordingly as the fifth step in the horizontal classification of patterns, under (5) general darkening of the wings including chiefly the exterior portions of the post-discal light band.

The vertical divisions of ground color, besides the dark fuscous pattern on portions of the wings, would naturally comprise two tints: different hues of russet, either of a bright brick tint or of an ochreous tone, and a basic whitish or ivory color, corresponding to *astorica* and *naryna* respectively. A pale ochreous tone, standing between these two types of coloration, called for a special subdivision which, however, does not comprise many forms. So the chromatic variation has been broken into three steps: russet, pale ochreous, and whitish, marked as A, B, and C. With the five possible variations of pattern, any form of *Karanasa* can be thus designated by these co-ordinates in a table covering fifteen fundamental types. It is to be noted that males and females of the same form do not fall on the same point of this table of color-pattern co-ordinates. To make the use of the table clearer, each intersection is illustrated by examples of typical males and females having such properties. That is how it happens that in the majority of cases the two sexes belong to different divisions in the table. The fifth group of "general darkening" does not lend itself with certainty to the attribution of russet, ochreous or whitish and in the case of "russet" could not be illustrated by any female. So there is no such insect which could be designated by the formula ♀ A5.

The advantages of this table lie not only in the simplicity of indicating the exterior aspect of a form by means of a symbol, expressed in a letter and a number; it helps also the appreciation of the range of variation, the component elements of variability, and also the deviation of a given type, in terms of color and pattern variations. Diagonal variations on the chart denote naturally the most extreme forms of instability involving a shift in both respects. Also the most extreme point on diagonal lines constitutes the greatest polarity of types as illustrated, for instance, by *wilkinsi* A1 and *kazakstana* C4 (excluding the fifth step) and *lactea* C1 and *kafir* A4. For instance, the amplitude of variations of *latefasciata* may be made graphically clear by extending into the three horizontal-chromatic-division in the fourth step of patterns A4, B4 and C4, with a tendency to deviate occasionally into B3.

A critical approach to this chart should not minimize a weak side of it, namely the mixed phylogenetic significance of the horizontal row B. The ochreous step, introduced merely for practical reasons to show graded differentiations, contains on the same levels entities which are not wholly comparable. Some of the ochreous forms are merely insects of the russet section that have acquired a paler aspect (like *leechi* and *decolorata*), or a regular whitish species, which has gained more color (like *ershoffi* and some females of *conradti*). For purposes of denoting actual kinship, the level B should be split into a fluctuating line of demarkation segregating only two basic color groups: russet (sometimes pale ochreous) and whitish (sometimes with a yellowish tinge). Grum-Grshimailo with his "keen entomological eye" perceived that it was enough to consider only two chromatic divisions.

As has been stated above, the chart accompanying this paper is used both for supplying a precise notation and for stimulating an analytical appreciation of analogous, but not homologous, properties falling into one category in accordance with the use of suggested coordinates. A compromise in this case is an invitation for a more comprehensive study.

Finally, it is interesting to note the statistical distribution of forms. Of the males, 45 (3/5ths) belong to A1-A4. The horizonal B and the vertical 5 both contain the least number of forms. In the A group the males fall predominantly into the divisions with higher numbers and the females belong mostly to the lower numbers in successive designations. For instance, in the division 4 there are males of several forms and very few females; these females belong to the preceding division 3; males of the 2nd and 3rd divisions often have females of division 1. In B and C the sexes are more closely paired in the various degrees of matching both as to coloration and pattern. Whether it could be an indication that the ancestral prototype fitted closer into these latter groups, as does the American *Neominois*, or that one should not attach any phylogenetic importance to these relationships, is a matter that could not be argued one way or the other on the ground of such considerations. At any rate the schematic table of patterns and colors simplifies and clarifies the revision of forms, and lends itself to interesting comparisons with other properties of the pattern on the underside of the hind wing.

In order to systematize the variations of the configuration of the marbled pattern on the underside, I propose the following method, based on the position and character of dented ante-marginal line e_3 of Schwanwitch, and the properties of the dark median band (plate 2). This ante-marginal toothed line is formed of outward pointed dentations or arrowheads between the veins. In some of the butterflies these points are sharp; in others they are blunted into crescents which tend to produce a scalloped effect. The position of this dented or scalloped line may vary; it occupies either the middle distance between the exterior margin of the darker median band and the edge of the wing, or else runs closer to the latter, approximately at one-third of the distance from the edge of the wing to the median band. These differences in position are respectively indicated by X and Y, and the acute or obtuse formation of the indentations are marked as a and o. A further notation of d and l for "dark" and "light" indicates the characteristics of inner portions of these arrowheads which might be darkened inwardly or traced on an even, light background. This element of the pattern is in close co-ordination with the character of the median band which may be either a shade darker than the general background, or else suffused with a marbled striation.

A further characteristic recorded in abbreviated notation is the prominence of the white veins: (1) for faintly seen veins (like *angrena*), (2) for a medium development (like *dissoluta*), and (3) for well accentuated white veins (like *aksuensis*). The notation of these traits of the underside is deemed sufficient, although one might also devise special notations for the variation of the pattern of the base which is either light or tends to merge in coloration and surface effect with the darker median band. It may be light as in *aksuensis* and, blending with the band into an even striation, spread throughout the whole basal half of the wing.

With these fundamental elements, a simple formula in letters and numbers can express the character of the underside and, together with the notation of the upperside in regard to color and pattern, may give an abbreviated, compressed description of the insect. For instance the *huebneri* male is ♂ A3 y d a v 2.

One could go further into the analysis of the underside of *Karanasa* in order to find a language of symbols for the most conspicuous traits—like the antemarginal portion of the front wings, the relative development of the pattern in the discus, and the characteristics of the ocelli. It seems, however, that the features pointed out so far will be sufficient for a proposed method of "algebraic" recording. Such a procedure of using a formula of conventional letters and figures could be easily applied and is recommended for a designation and analysis of forms in any related group.

For comparative clarity a typical section of the hind wing is taken into consideration from vein Cu_2 to the middle of the next interspace and inwardly as far as the inner edge of the median band. This irregular section is reduced to a rectangular conventionalization so as to show the characteristics of the band and the position and aspect of the antemarginal zig-zag line. In such a fashion each form is reduced to an even and comparable rectangular band as shown on plate 2. It can enable one to see at a glance the elements that are recorded in the system of schematic notations and group similar forms together. Other important characters, the formation of the band and the aspect of the base, are too variable for a system of notation, which might tend to become unduly complex.

One of the pioneers of a study of patterns reduced to co-ordinates in a rectangular conventionalization was Riffart, who analyzed the pattern of *Heliconia* and prepared illustrations which look like a species of lepidopterological cubism. The illustrations in plate 2, where patterns are reduced to tags, is a less extreme adaptation of the same principle where the actual pattern remains sufficiently recognizable within moderate conventionalization. The Heliconids in the "pictograms" of Riffart, on the other hand, require a considerable stretch of the imagination to visualize the actual insects. It proves, perhaps, that the rule of geometry over lepidopterology should not be overly dictatorial where the interests of visual recognition have to be safeguarded.

While it is aside from any proposed system of marking, it is considered of interest to illustrate a comparison of a few typical bands in *Karanasa* with those of *Neominois*, *Satyrus* and even such a distantly related genus as *Neope*, as an example of the extreme complexities in the development of the band. Schwanevitch[1] made some extensive studies of significant and component elements of the pattern of the underside of the hind wings in Satyrids. His conclusions on the identity of different parts of the pattern undergoing fluctuations, dislocations, and fusion are highly instructive.

[1] Schwanwitsch, B. N. "Evolution of the Wing-Pattern in Palearctic Satyridæ" "I. Genera Satyrus and Oeneis." Zeit. Morph. Oekel. Tierre; Berlin, Vol. 13, pp. 559-654, 1929.

It suffices to state here in this conjunction that the median band traversing this discocellular is based on a phenomenon of certain symmetry in the pattern of the basal and external part of the wing. Thus for the Satyrids, as well as for the related group of Nymphalidæ, Brassolidæ, and Morphidæ, one may accept as typical a medium dark band edged symmetrically, inwardly and outwardly, by a lighter line and a darker outline, as is clearly seen in *Neope*. These elements may become partly broken up by veins and the double margin preserved for each open cell, or else they are undisturbed by the venation. A comparison of *Neope muirheadi* with three other species of the genus illustrates those two varieties of reaction of the pattern to the presence of veins (plate 2). It demonstrates the relative— not absolute— dependence of the pattern on anatomical properties of the surface of the wing, namely, the arrangement of veins, and it may show to a considerable degree what may be termed organic autonomy of the pattern. In *Karanasa* the band does not display such regularity of pattern structure and is of interest mainly by its outline obeying some standard fluctuations within cellular outlines. A comparison of *Karanasa* and *Neominois* in this respect is instructive. In *Neominois* the tooth in space M_2-M_3 is the most prominent, while in *Karanasa* it is the one above in space M_2-M_1. Furthermore, in space Cu_2-Cu_1 in *Neominois* the band is distinctly narrowed, but usually of the same width as the rest of the band in *Karanasa*. A constriction of the band in this point is typical for some forms of the *conradti-regeli* group, namely in *turugensis* and *arpensis* and in *korlana* to a lesser degree. This trait is also observed in *Satyrus geyeri* and it may be taken perhaps as a sign of some primitive character for a whole group of related Satyrids. It may be another indication that it is the *conradti-regeli* type which corresponds to the ancestral form related to the American *Neominois* and somewhat similar to another far more removed branch exemplified by *Satyrus geyeri*.

The upper part of the band calls for special considerations. The portion between the first and second subcostal in *Karanasa* tends to be outlined by a concave contour on either side with an extension outwardly along the 2nd subcostal. In *Neominois* the formation is reversed constituting a convex outline that produces an oval marking in this interspace. This divergence is demonstrated on plate 2 and has certain phylogenetic implications. The band formation of *Karanasa* is in closer correspondence to the predominantly even or parallel outlines in the pattern of Satyrids in general. The comparison with *Satyrus* and *Neope* is a confirmation of this effect. So, the formation of the band in *Karanasa* may be considered more primitive than the alteration in *Neominois*, especially in certain extreme specimens of *N. dionysius*. The interpretation of the peculiarities in the relative formation of the upper portion of the band in *Karanasa* and *Neominois* requires a more thorough scrutiny. The extension into outward points between the veins in the whole exterior outline of the band is characteristic in both genera and is shared by *Satyrus geyeri* as well. In the interspace below the second subcostal, the outline of the band shows a vestige of this point in *Karanasa*, just below the extension along the vein. One may consider that the point situated in the middle of this interspace in *Neominois* has relatively moved upward and has produced a partial disappearance of this protrusion together with an extension alongside the vein. It corresponds to the general shift of the pattern upward toward the costa, thus effecting in *Karanasa* a constriction of the band, while in *Neominois* this part of the pattern shows central inflation, producing between the veins an isolated oval spot. A shift of pattern, independent of the anatomical properties of the wing, falls into the general category of the peculiar phenomenon designated as "pierellisation" by Schwanevitch. It was described as a particular dislocation of bands and ocelli in the South American Satyrid genus *Pierella*. Schwanevitch observed and singled out analogous phenomena in a number of cases. Something analogous occurred in the genus *Karanasa*, and it may be assumed that the conservative trends in the formations of the band were complicated and supplemented by an evolutionary process expressed by a slight shift of the pattern toward the costa.

The character of the surface treatment of the band in *Karanasa* may vary substantially from being almost as light and uniform as the rest of the background of the wing, as in *wilkinsi* and *intermedia*, to an even darkening as in the *decolorata* group, or to a marbled aspect as in *alpherakyi*. Such a reticulation is, in fact, of a dual nature. In part it is the remnants of the shuffled outlines of the inner portions of the band so clearly exemplified in *Neope;* and in part it is the ancestral vermiculation of large areas in the underside of Rhopalocera, of which the family Elymnidæ is the most typical. Such a pattern is evidence of the loss of the numerous transverse veinlets of the primitive Neuropteroid insects which preceded the development of Lepidoptera. Primitive forms of Lepidoptera show well these surviving scars of lost veins, in the pattern, as in the family Cossidæ, for instance. The preservation of such a transverse reticulation in the costal region of the front wings, not only of Nymphalids and Satyrids but even in Pierids, is symptomatic of this origin, as has been frequently stated in entomological literature. The costal region is supposed to have preserved certain atavistic traits in terms of pattern. The strongly marbled base of the hind wings, including the band, in the *pamira* group and in other forms as shown on plate 2, is at least in part an atavistic character of this order and not merely a splitting and dislocation of identifiable linear bands. It is practically a double phenomenon of the same order as the case of *Caligo*, where the general over-all reticulation condenses itself to suggest the shading of typical, individual, ante-marginal bands in zig-zag formation. Analogously, through the maze of an irregular striation in the *pamira* group of *Karanasa*, one can easily discern the inner outlines of the median band and the accentuation of the usually obscured basal band.

In one more point the underside of the hind wing of *Karanasa* requires some study, namely in regard to vestigial ocellation. The primoridal type of the Nymphalo-Satyrids possessed presumably a complete row of ocelli between the median band and the ante-marginal arcuated line. Parenthetically it should be mentioned that these ocelli in their own turn were a modification and confluence of two bands, transformed into isolated links. In *Neominois* there are no traces of such ocelli, while in *Karanasa* they appear in rare instances (in *abramovi* and *talastauana* groups) on the upperside between the first and second radial. On the underside, vestiges of ocelli may be observed as faint white spots just within some of the ante-marginal arrow points as seen in diagrams in plate 2.

Probably the closest approach to an abortive ocellus is observable in *safeda* which shows a dark outline of this white center. So here we see in *Karanasa* an ancestral trait which has been lost in the American branch of the group. The presence of such vestigial pupils of lost ocelli in the most primitive *Karanasa* of the *regeli* group should not be overlooked from the phylogenetic angle. Altogether one might sum up the characters of the *Karanasa* underside as a typical Satyrid pattern somewhat impoverished, and with a slight upward dislocation of the hind wing pattern. The utmost of simplification is reached in *intermedia*, which constitutes the extreme manifestation of a gradual loss of patern on the upperside, with a predominant russet hue always remaining as one of the two most typical chromatic possibilities in the family of Satyridæ. From these various grounds it would be justifiable to consider *intermedia* as the most progressive type in the evolution of the *Karanasa* group.

The fluctuations between the highly pigmented scales with a russet hue and the tendency toward a whitish color is to be seen in the whole realm of Satyrids. It may be individual within certain species like *Satyrus anthe* and *briseis* where the white and ochreus-orange morphs appear as aberrations or mutations. It may be a sexual trait, as in *Lethe.* On the other hand, the color principle may be a matter of established stability such as the white background of *Melanargia* or the russet bands of *Epinephele.* In our group the coloration is in itself a trait of uneven phylogenetic value. The lighter background—less pigmented with ochreous and russet—acquires a more ancestral significance only in conjunction with more archaic pattern traits. It is only in this spirit that one should advance the arguments in favor of the antiquity of the whitish *conradti-regeli* group, recording at the same time the phenomenon of wide chromatic variation within the species *grumi* and the group *pamira-alpherakyi,* both of which groups may include either whitish or bright russet forms. It proves only that the pattern and color traits are not of equivalent value as factors of heredity; but both should be considered in their interplay of relative significance.

EXPLANATION OF PLATE 1

Table of standards for the classification of the colors and patterns in the genus *Karanasa*. Plate prepared by A. Avinoff.